>>> Tim O'Laughlin <towater@olaughlinparis.com> 2/23/2011 9:32 AM >>>

Mr. Grober & Ms. Riddle:

We did not see the attached report cited in your Draft Technical Report. One of the conclusions of this peer-reviewed article is: “The lack of any detectable effect of hydrology on autumn run salmon is, perhaps, surprising given that this factor is frequently cited as a major contributor to the loss of Chinook salmon in the Central Valley of California, and RE-CREATION OF HISTORICAL HYDROLOGICAL CONDITIONS IS A FOCUS OF MANY RECOVERY EFFORTS (United States Fish and Wildlife Service 2001).” (Emphasis added) p.8.

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Predictors of Chinook salmon extirpation in California's Central Valley

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Abstract Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum), populations have declined rapidly along the western coast of North America since the year 2000, possibly because of factors such as habitat loss, altered hydrology and barriers to migration. However, few analyses have rigorously examined which of these factors actually explain historical patterns of extirpation. Data were compiled on flow regimes, habitat loss and migration barriers for 27 streams that historically supported autumn run salmon and 22 streams that supported spring runs. The probability of extirpation in streams supporting autumn run was predicted solely by migration barriers. All other factors were $>10^5$ times less likely to explain existing variation. By contrast, models for spring run salmon suggest that habitat loss and altered flow regimes were also predictors of extirpation. These results suggest that regional extirpation of Chinook salmon has been driven by multiple forms of environmental change, and restoration efforts must address a multitude of bottlenecks that now impact spring and autumn run populations.

KEYWORDS: dam, habitat loss, hydrology, Sacramento, San Joaquin.

Introduction

Pacific salmon (*Oncorhynchus* spp.) is an important economic, recreational and cultural resource throughout its geographical range. Although total production of some species has increased during the 20th century (Schindler *et al.* 2008), populations in many regions have experienced major declines and an estimated 29% of all salmon populations have been extirpated from the Pacific Northwest and California (Gustafson *et al.* 2007). Loss of local populations has reduced the range of life-history characteristics and genetic diversity of species, which could limit the ability of salmon to adapt to climate change and, ultimately, limit the long-term viability of some species (Moyle 1994; Crozier *et al.* 2008). Populations at greatest risk tend to occur in interior as opposed to coastal regions (Gustafson *et al.* 2007). Additionally, the biological consequences of extirpation are high for populations that occur at the extremes of the species range distribution because these populations often have unique biological adaptations, such as tolerance of extreme temperatures, that

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disproportionately contribute to the genetic diversity of the species relative to populations in the middle of the species' range (Allendorf *et al.* 1997). The Central Valley of California is an interior region that supports the southernmost spawning populations of Chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Thus, conservation of these populations has been deemed a high priority to maintain the genetic and life-history diversity of Chinook salmon that is essential to the long-term persistence of the species (Ruckelshaus *et al.* 2002).

A recovery plan has been implemented for Central Valley salmon (USFWS 2001) that includes Chinook salmon. However, the goal of doubling natural production has not been reached, and instead, many populations continue to decline. Part of the problem is that many recovery plans lack basic information on the nature of threats, complicating attempts to prioritise restoration strategies (Lawler *et al.* 2002). A common problem in salmon recovery plans is that data available for assessment and decision-making by policy makers are often qualitative, consisting of professional opinion- or semi-quantitative, consisting of extrapolated or inferred data integrated with empirical measurements (Ruckelshaus *et al.* 2002). Although threats to Central Valley salmon are well known (Moyle 1994), attempts to quantify the relative importance of these threats and rank potential restoration strategies have been largely lacking. Thus, Boersma *et al.* (2001) suggested that explicit science designed to prioritise risk and address specific questions is needed to improve the recovery process for threatened and endangered species.

An information theoretical approach was used to evaluate quantitatively the weight of evidence for three hypotheses that are commonly proposed as explanations for the extirpation of Chinook salmon in the Central Valley of California. The first hypothesis is that migration barriers best explain extirpation where streams above barriers no longer support salmon and below barriers, salmon continue to persist. The second hypothesis is that habitat loss – in terms of length of river kilometres still accessible to salmon – best explains extirpation. The mechanism underpinning this hypothesis is that smaller habitats support fewer individuals that, in turn, increase the chance that demographic or environmental stochasticity will result in extirpation. The third hypothesis is that flow regimes have been altered such that they no longer support salmon. The mechanism underpinning this hypothesis is that post-regulation flow regimes have created conditions that reduce survival such as stranding of juveniles and dewatering redds (Ugedal *et al.* 2008), and reduced or eliminated access to favourable habitats such as floodplains (Sommer *et al.* 2001). Thus, streams where salmon persist have different flow regimes than streams where salmon have been extirpated.

Quantitative evaluations of these hypotheses were conducted for both spring run and autumn run Chinook salmon. These two runs were historically the most widely distributed in the Central Valley of California and represent distinct life-history types. Life-history characteristics have been shown to influence strongly extirpation probabilities for other at risk fish species (Olden *et al.* 2006). Autumn run salmon enter freshwater streams during a period from late summer through autumn and spawn soon after reaching suitable habitat. In winter and early spring, juveniles emerge from the benthic habitat, where eggs are laid and alevins are hatched and rear in fresh water for weeks to several months before starting their migration to marine waters (ocean-type life-history). Spring run salmon enter freshwater systems from spring to early summer and inhabit pools throughout the summer before completing maturation and spawning in early autumn. Juveniles may follow an ocean-type life-history similar to autumn run or they may spend a full year in fresh water before migrating out of the system the following spring (stream type life-history).

Methods

Study system

The Central Valley of California extends approximately 600 km from the Cascade Mountains in the north to the Tehachapi Mountains in the south. The eastern border of the valley is the Sierra Nevada Mountains and the Coast Range forms the western boundary. The Sacramento and San Joaquin rivers are the two principal river basins draining an area of approximately 69 930 and 82 900 km^2, respectively. The Sacramento River drains the northern portion of the valley and runs north to south, whereas the San Joaquin River drains portions of the southern valley and runs south to north. Both rivers terminate in the San Francisco Estuary in an area known as the Sacramento-San Joaquin Delta. The principal tributaries of the Sacramento enter from the east and drain the western slope of the Sierras and portions of the southern Cascades. Tributaries draining the Coast Range are less substantial but several support Chinook salmon populations. Major tributaries of the San Joaquin also drain the western slope of the Sierras. Unlike the Sacramento basin, tributaries entering the

San Joaquin from the Coast Range are generally intermittent and are unlikely to have ever supported salmon populations (Yoshiyama *et al.* 2001).

Aquatic habitats in the Central Valley have a long history of modification associated with human activities. Extensive gold mining in the mid 19th century severely degraded many rivers through the addition of large volumes of fine sediments, mercury pollution and construction of barriers to salmon migration. Historical accounts suggest that these activities had a large impact on salmon populations, although they have seldom been quantified (Yoshiyama *et al.* 2001). During the 20th century, a large number of dams and diversions were constructed on Central Valley streams to support agricultural and urban development. Most of these dams are total barriers to salmon migration preventing access to productive spawning and rearing habitats. Additionally, dam operations have altered the natural flow regimes of downstream reaches that remain accessible to Chinook salmon.

Data used to address hypotheses

Evaluation of the three hypotheses presented in the introduction required that several types of data to be available for a stream: (1) records of the presence of salmon prior to the era of anthropogenic alteration (historical data) and modern day (period following completion of most major dams) presence or absence; (2) height of potential barriers to salmon passage; (3) estimates of the amount of river kilometres lost because of impassable barriers; and (4) flow data for a period sufficient to characterise reliably the hydrological dynamics of the stream. Historical and current distributions of Central Valley Chinook salmon and estimates of habitat loss (% river kilometres) were obtained from Yoshiyama *et al.* (2001) and National Marine Fisheries Service (1999). The historical data were compiled from a variety of sources including early agency reports, newspaper articles, accounts of settlers and interviews with biologists. Modern day distributions primarily consist of agency reports and published papers. Yoshiyama *et al.* (2001) and NMFS (1999) provide details on the various data sources.

Salmon were recorded as extirpated if historical records indicated that a stream was used by salmon during at least one life-stage, but modern day assessments indicate they are absent. Salmon was recorded as extant if at least one life-stage continues to use the stream (Fig. 1). Habitat loss was estimated as the percent of river kilometres lost in each stream calculated from the stream mouth to the estimated upstream distribution limit. The height of potential barriers was obtained from the California Department of Water

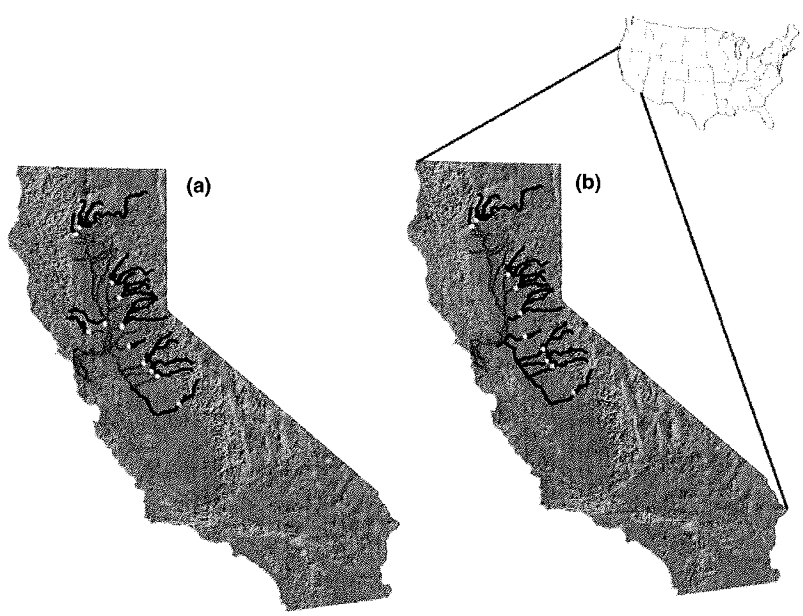

Figure 1. Maps depicting all streams that conformed to data requirements for analysis of autumn run (a) and spring run (b) Chinook salmon extirpations. Streams in red continue to support autumn run salmon. Streams in black historically supported salmon but have been extirpated. Yellow circles indicate the location of dams within the historic range of salmon that are total barriers to migration. When multiple streams were located above a dam, only the north fork was included in statistical models.

Resources Division of Safety of Dams. Barriers greater than 2.4 m that did not contain fish passage facilities were assumed to be too high for salmon to pass [which is roughly the height that Chinook salmon can jump (Bjornn & Reiser 1991)] and thus were barriers to upstream migration.

Data on flow regimes were obtained from the US Geological Survey (USGS) that operates a network of flow gauges throughout the Central Valley. Thus, for a stream to be included in the data set, it had to be gauged by the USGS. Most gauges were located downstream of dams near the modern distributional limits. When rivers contained more than one gauge, the gauge nearest to the distribution limit was selected. A 30-year period of record (1973–2003) of daily stream flow was selected to represent the modern flow regime. Flow regimes can change considerably in a 30-year time period. Nevertheless, records comprising several decades are required to estimate accurately the probabilities of infrequent events such as floods and extreme low-flows that may be important to the persistence of salmon. The analyses were only dated back to 30 years because the period after 1973 represents a time when all major dams were completed in the Central Valley, and nearly all land had become dominated by agriculture. The records were ended at 2003 because this was the last year for which flow data were cross checked and validated by the USGS when the analyses were performed.

A suite of 12 flow regime descriptors was calculated from mean daily flow records to represent the four broad categories of flow variability identified by Poff and Ward (1989) as influencing lotic taxa at regional scales: basin descriptors, overall flow variability, pattern of the flood regime and extent of extreme low-flows (Table 1). These 12 flow descriptors were previously used to categorise the life-history characteristics of stream and river species that occupy different flow regimes in North America (Poff & Ward 1989; Puckridge *et al.* 1998). As such, the 12 descriptions were used to describe the impact of flow regimes on everything from algae to invertebrates to fish. Many of the hydrological variables were correlated with one another, thus the variables were reduced into orthogonal axes of variation using principal components analysis (PCA using CANOCO Version 4, Microcomputer Power). Separate analyses were performed for the spring and autumn run streams. All subsequent analyses used PCA scores on the first two axes (which explained 78–83% of all the variation in hydrology among streams) in place of individual variables. These axes had biological interpretations that are described in the next paragraph.

Table 1. Flow regime descriptors used in principal components analysis. Descriptors were calculated from 30 years of mean daily flow data (1973–2003) obtained from U.S. Geological Survey flow gauges

Variable name	Definition
Basin descriptors	
Area	Drainage area (km^2)above the stream gauge
MAF	Mean annual flow from 1973 to 2003
SS	Size scalar–MAF/area
Flow variability	
Co/month	Colwell's predictability index for mean monthly flow
CV/month	Coefficient of variation of mean monthly flow
Flow/month	Log-transformed mean flow in each month
Pattern of the flood regime	
Co/flood	Colwell's predictability index for floods
FI	Flood interval – mean number of days between floods
TSR	Total slope rising – average slope of the rising limb of floods
Season/flood	Season with the greatest mean number of floods
Extent of low flows	
LFI	Low-flow interval – average number of days between low-flow periods
Season/low	Season with the greatest mean number of low-flow events

To augment the interpretation of select hydrological patterns, the modification of historical flow regimes by dams was characterised for five rivers where there were sufficient pre- and post-dam data available. Only five rivers had mean daily flow records for a 30-year period prior to dam construction in addition to a 30-year period after dam construction. The influences of dam construction and initial operation on flow data were avoided by excluding 8 years of data immediately prior to and immediately following the year of dam completion from the 30-year period.

Two data sets were constructed for the two most widely distributed Chinook salmon runs – spring and autumn. There were sufficient data to include a total of 27 streams in the autumn run data set and 22 streams in the spring run data set (Fig. 1). Some streams for which data were available were excluded from analysis because of a lack of independence. This occurred when more than one fork of a river was upstream of a total barrier to migration. When this occurred, only the north fork was selected simply as a consistent means for inclusion in the data set.

Data analysis

A series of logistic regression models was constructed to test the three hypotheses proposed to explain the probability of Chinook salmon being extirpated from Central Valley Rivers. For all models, the response variable was salmon status (1 = extant, 0 = extirpated). Predictor variables included: location of the stream relative to a barrier (1 = downstream, 0 = upstream), percent of river km lost, sample scores on principal component axes 1 and 2 that describe the major axes of hydrological variation. Separate model sets were constructed for the autumn and spring run. All models were constructed in SAS (Version 9.1.3, SAS Institute Inc., Cary, NC, USA).

Best approximating models were selected for spring and autumn run data sets using an information theoretic approach. Akaike's Information Criterion corrected for small sample size (AIC_c) was calculated for each candidate model. The difference in AIC_c values between the best model and competing models (ΔAIC_c) was used to calculate AIC_c weights and evidence ratios. Model weights are interpreted as the probability that a particular model is the best fit to the data relative to all other models being considered. Evidence ratios indicate the level of support for two or more competing models based on AIC_c weights. Thus, using AIC_c weights and evidence ratios, it was possible to evaluate the relative weight of evidence for or against each of the three hypothesised causes of Chinook salmon extirpation.

It was not possible to conduct a rigorous statistical analysis to test whether the probability of Chinook salmon extirpation could be linked to specific hydrological changes imposed by the construction of a dam because of the small number of rivers that had both pre- and post-dam flow records. Nevertheless, pre- and post-dam flow records were used to make several qualitative comparisons that, despite the lack of any direct statistical test, can be used to raise new hypotheses about why changes in hydrology may have influenced salmon at different life stages.

Results

Autumn run

Autumn run Chinook were extirpated from seven streams but persist in 20 streams. All streams where Chinook salmon were extirpated were upstream of structures that are barriers to salmon migration (Fig. 1a). Models that predicted expiration of autumn run salmon included habitat loss and migration barriers as parameters (AIC_c weights ≥0.48 and evidence ratios ≤ 1.08), whereas all other models were poor predictors (model weights <0.01 and evidence ratios >1 000 000) (Table 2). The model that included habitat loss was well supported because 100% habitat loss predicted extirpation as well as the location of a stream relative to a migration barrier. It is not at all a surprise that migration barriers can explain salmon extirpation. What was surprising from the analysis was complete lack of support for any other explanation or hypothesis for extirpation of the autumn run.

Table 2. Best approximating models for autumn run Chinook salmon. Models are arranged from best to worst based on evidence ratios. AIC weights are the relative likelihoods of a model given the data, and evidence ratios are the relative likelihood of each model vs the best model

Model	Variables in model	AIC_c	ΔAIC_c	AIC_c weight	Evidence ratio
2	Lost km	4.89	0.00	0.52	1.00
1	Barrier	5.04	0.15	0.48	1.08
4	PC1	33.31	28.42	0.00	1 482 221.23
3	PC1, PC2	33.87	28.98	0.00	1 959 679.47
5	PC2	33.98	29.09	0.00	2 068 951.16

Despite the poor performance of hydrological-based models to predict Chinook salmon extirpation, PCA explained 78% of the total variation in 12 hydrological variables among the 27 streams. Axis 1 determined 56% of the variation and differentiated streams with long intervals between floods and extreme low-flows, greater flood predictability and greater flows in summer and autumn from streams with greater monthly flow variability and spring flooding. Axis 2 (22% of variance explained) differentiated large streams with greater mean annual flow and flow predictability among months from smaller streams with steep flood profiles and greater flows during winter. Although there was variation in flow regimes among streams captured by PCA, these differences were insignificant relative to the presence of barriers in predicting Chinook salmon extirpations.

Spring run

Spring run Chinook salmon were extirpated from 12 streams and continued to persist in 10 streams (Fig. 1b). Model selection indicated that both migration barriers (AIC_cW = 0.64, ER = 1.00) and habitat loss (AIC_cW = 0.25, ER = 2.55) were well supported as predictors of extirpation (Table 3).By contrast to the autumn run, one of the hydrology models (predictor = PC1) had a sufficient level of support in the

Table 3. Best approximating models for spring run Chinook salmon. Models are arranged from best to worst based on evidence ratios. AIC weights are the relative likelihoods of a model given the data, and evidence ratios are the relative likelihood of each model vs the best model

Model	Variables in model	AIC_c	ΔAIC_c	AIC_c weight	Evidence ratio
1	Barrier	24.90	0.00	0.64	1.00
2	Lost km	26.78	1.88	0.25	2.55
4	PC1	29.09	4.19	0.08	8.10
3	PC1, PC2	31.86	6.96	0.02	32.31
5	PC2	33.36	8.46	0.01	68.44

Table 4. Best approximating models for spring run Chinook salmon in rivers located below migration barriers. Models are arranged from best to worst based on evidence ratios. AIC weights are the relative likelihoods of a model given the data, and evidence ratios are the relative likelihood of each model vs the best model

Model	Variables in model	AIC_c	ΔAIC_c	AIC_c weight	Evidence ratio
3	PC2	21.59	0.00	0.59	1.00
4	PC1, PC2	22.16	0.57	0.44	1.33
2	PC1	23.29	1.70	0.25	2.34
1	Lost km	24.19	2.60	0.16	3.67

analyses to prevent its exclusion as a viable hypothesis ($AIC_cW = 0.08$, ER = 8.10). The spring run PCA determined 79% of the total variation among streams and described the same relationships as the autumn run PCA. Thus, compared with autumn run Chinook salmon, the probability of spring run extirpation was less clear with models supporting migration barriers, habitat loss and possibly changes in stream hydrology as potential contributors to extirpation.

The potential role of hydrology in predicting extirpation was explored with a model selection exercise that excluded streams upstream of migration barriers. A third PCA was performed that included only the streams downstream of a barrier. A total of 16 streams were included in this analysis. Chinook salmon were extirpated from six of these streams and persisted in 10. Models that included hydrology were stronger predictors of extirpation than was habitat loss ($AIC_cW \geq 0.25$, ER ≤ 2.34); but habitat loss remained a competing predictor (Table 4). The best approximating model included PC 2 as the predictor variable, and all streams with positive scores on PC 2 continued to support spring run salmon populations (Fig. 2). Streams with positive scores on Axis 2 had steeper flood profiles, greater flows in late autumn and early winter and longer intervals between extreme low-flow periods. Streams with negative sample scores were larger and had greater flows during summer and early autumn. The difference in the strength of models that use hydrology to predict extirpations of spring run Chinook salmon below barriers suggests that autumn and spring run salmon may respond differently to changes in hydrology and habitat loss following the construction of dams.

The analysis of post-dam hydrological changes suggested that dams may be reducing stream flows

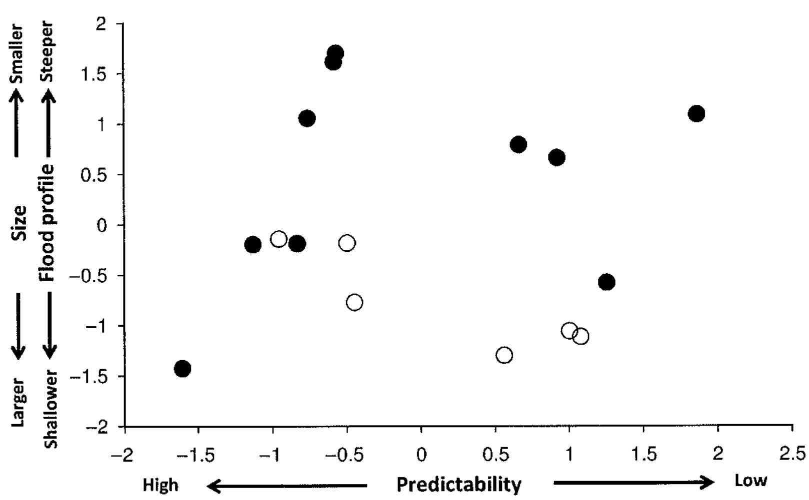

Figure 2. Bi-plot of sample scores on principal components PC1 (abscissa) and PC2 (ordinate). All streams used in the analysis historically supported spring run Chinook salmon and are located below barriers to migration. Closed circles represent streams where Chinook salmon persist, and open circles represent streams where they have been extirpated. Variables that loaded strongly on axis one included Colwell's predictability index for floods and monthly flow, drought interval and the coefficient of variation for monthly flow. Variables that loaded strongly on axis 2 included mean annual flow, drainage area and the slope of the rising limb of flood events.

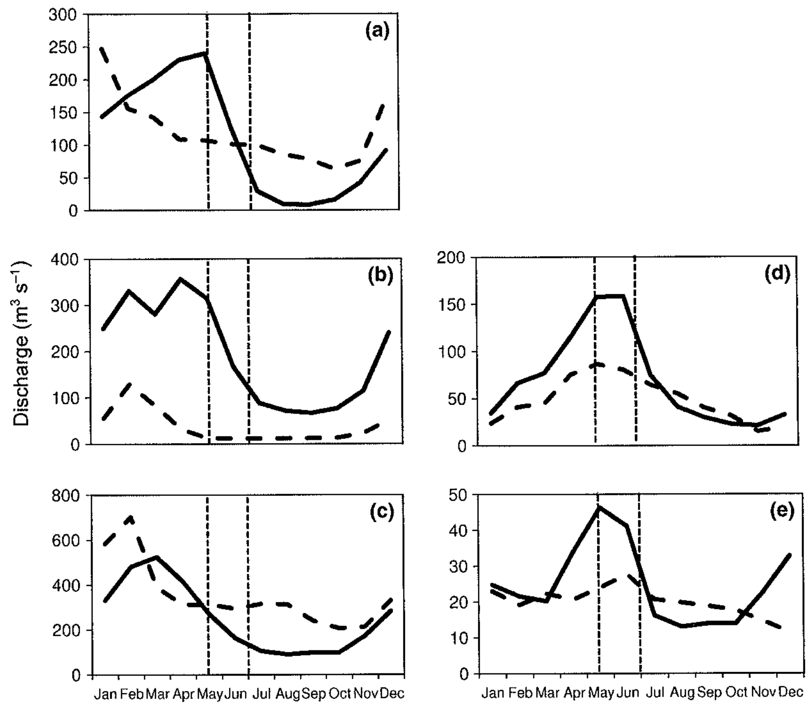

Figure 3. Pre- and post-dam hydrographs for five Central Valley rivers. Solid lines are mean monthly discharge values for 30 years prior to dam construction. Dashed lines are mean monthly discharge values for 30 years after dam construction. Vertical dashed lines indicate the peak period of spring run migration. Note that the discharge scales (y-axis) differ between the graphs, that the peak migration period corresponds to the peak or declining limb of floods in the pre-dam hydrograph and that these discharge pulses have been attenuated or shifted outside of the migration period in the post-dam hydrographs. Rivers: a, American River; b, Feather River; c, Sacramento River; d, San Joaquin River and e, Mokelumne River.

during a critical period when spring run Chinook salmon are trying to migrate upstream and that this change may be contributing to extirpation. Monthly stream flow data before and after dam construction were available for only five Central Valley streams (Fig. 3). Two streams were located in the San Joaquin basin (Mokelumne River and San Joaquin River) and three were located in the Sacramento basin (Sacramento River, Feather River and American River). Of the five streams, only the Feather and Sacramento continue to support spring run salmon, but the Feather River run is strongly supported by hatchery production (Lindley *et al.* 2004). All five streams support autumn run salmon, but the San Joaquin is currently used only as a migration route to spawning tributaries.

Plots of mean monthly flows suggested that dams imposed major changes in the hydrograph of all five streams. A similar pattern of alteration was observed in four of the five rivers where water is held back during winter and spring months resulting in an attenuated flood pulse, and released during summer and autumn producing higher flows than prior to dam construction (Fig. 3). In the Feather River, flows were reduced during all seasons (Fig. 3). Attenuation of annual flow pulses may have impacted the persistence of spring run populations because migration of spring run salmon coincides with periods of peak flows or during the declining limb of high-flow periods in the pre-dam hydrographs (Fig. 3). The Sacramento was the only river with greater flows during the spring migration period and spring run fish continue to persist in this river. Flows during the summer holding period were greater in the three streams where spring run salmon have been extirpated, as well as the Sacramento, and lower in the Feather where they persist. Effects of flow regulation during the autumn spawning period were mixed, but autumn run fish continue to spawn successfully during this period except in the San Joaquin.

Discussion

Data were compiled on historical and modern Chinook salmon distributions, habitat loss, barriers to migration and flow regime to test the weight of evidence for three hypotheses that are commonly posed to explain the loss of Chinook salmon in the Central Valley. The persistence of autumn run Chinook salmon was predicted by their location relative to migration barriers. The negative effect of barriers on upstream populations of migratory fishes is well known; thus, it is not surprising that dams have the potential to explain extirpation of these, or other migratory fishes (Gehrke *et al.* 2002; Morita & Yamamoto 2002). What was surprising is that there was no evidence that other hypothesis considered had the potential to explain Chinook salmon extirpation for the autumn run. The hypothesis that altered hydrological regimes led to extirpation had no ability to explain patterns in the data (> 1 000 000 times less likely than barriers), and this was true despite there being wide variation in hydrological conditions among streams and that pre- and post-dam comparisons revealed substantial changes in hydrology. The lack of any detectable effect of hydrology on autumn run salmon is, perhaps, surprising given that this factor is frequently cited as a major contributor to the loss of Chinook salmon in the Central Valley of California, and re-creation of historical hydrological conditions is a focus of many recovery efforts (United States Fish and Wildlife Service 2001).

Migration barriers and habitat loss were competing predictors of spring run salmon extirpation, and flow regime was a strong predictor among rivers that remain accessible. Thus, the best predictors of extirpation depended on the population of rivers used in the analysis. Spring run Chinook salmon historically used higher elevation habitats (> 150 m) where temperatures remain cool during the summer holding period (Yoshiyama *et al.* 2001; Lindley *et al.* 2004). Most of this habitat in the Central Valley has been lost through construction of impassable dams. Restriction of spring run salmon to lower elevation habitats used by autumn run salmon also may reduce genetic distinctiveness as has been inferred from studies of the Feather River Chinook populations (Lindley *et al.* 2004). The greater influence of habitat loss on spring run salmon extirpation probabilities may be accounted for by this difference in habitat use and needs to be considered when formulating recovery strategies.

Hydrological regime was also a strong predictor of spring run salmon extirpation below migration barriers, with extant runs found in smaller streams that retained a steep flood profile. Spring run salmon enter fresh water from spring through early summer during high flow periods and hold in the river over summer before spawning in autumn. By contrast, autumn run salmon spawn soon after entering fresh water in late summer and autumn. The longer period in fresh water may expose spring run salmon to risks that are not experienced by autumn run Chinook salmon (Williams 2006). However, the analyses suggested that greater flow during the summer months was associated with streams where spring run Chinook salmon had been extirpated. Additionally, three streams where spring run salmon were extirpated had greater summer flows in the post-dam period. The period of spring run migration appeared to be an important component of the hydrological regime. Streams where spring run salmon persist were associated with steeper flood profiles and the peak of spring run salmon migration occurs during peak flows or on the declining limb of pre-dam hydrographs. Post-dam hydrographs revealed a common pattern among the few regulated rivers in the Central Valley where sufficient historical data are available; that pattern suggested that high flows in spring are stored in reservoirs and released during summer for diversion downstream. High flows provide an important spawning cue for some species (Zeug & Winemiller 2007; Bailly *et al.* 2008) and the loss of this aspect of the flow regime may have contributed to the extirpation of spring run salmon. Only the Sacramento River had greater flows during the migration period post-regulation, and spring run salmon continue to persist in this system.

Limits to inference

The analyses presented have focused somewhat narrowly on the presence or absence of salmon in streams. Limitations in data quality and availability prevented the use of measures of abundance or population growth rate of Chinook salmon as dependent variables. This leaves open the possibility that some factors considered could still be leading to declines of Chinook salmon, even if the species is not yet locally extirpated. This is potentially important because although barriers cause rapid extirpation of upstream populations, downstream populations may experience long periods of decline prior to extirpation (Kareiva *et al.* 2000). Schick and Lindley (2007) found that barrier-related extirpation of certain spring run salmon populations in the Central Valley had a disproportionate effect on the remaining populations because of source-sink dynamics. Additionally, the large number of Chinook salmon produced by hatcheries in the Sacramento-San Joaquin system may prevent extirpation through the straying of returning adults. Genetic data from spawning populations in the Central Valley indicate little differentiation between hatchery and natural spawning Chinook salmon and low heterogeneity among individuals collected from different rivers suggesting extensive straying of hatchery fish (Williamson & May 2005). Barnett-Johnson *et al.*

(2007) found that large numbers of Sacramento and San Joaquin salmon taken in the ocean fishery were of hatchery rather than wild origin (84–96%). If similar percentages of returning adults are of hatchery origin, natural populations in the rivers that remain accessible may not be self-sustaining.

The information theoretic approach was limited in that it only evaluated the weight of evidence among the given hypotheses; thus, the possibility that other hypotheses not evaluated here could prove to be a better fit to the data cannot be eliminated. Hypotheses such as competition with and predation by non-native species, changing stream temperature regimes, availability of appropriate spawning and rearing substrate and a myriad of others have also been proposed to explain patterns of Chinook salmon loss. While data regarding these hypotheses were not available at the scale of the current analysis, one of the advantages of the information theoretic approach is that as data become available, it is straight-forwarded to pit explanatory variables against one another and decide which is the better potential explanation. As analyses are improved, it is worth noting that some hypotheses may only be the proximate causes of extirpation while several of the ultimate causes (barriers, habitat loss and altered flow regimes) were captured by the analysis. For example, barriers have constrained spring run to reaches that may not provide the appropriate temperatures during the summer holding period (Williams 2006). Additionally, dams prevent the movement of spawning gravel from upstream areas and attenuate flood pulses that are essential for the geomorphological development of rearing habitat for juveniles. Despite the limitations of the current approach, the evidence suggests that dams increase the probability for extirpation of Chinook salmon by blocking migration routes (autumn run), constraining the amount of habitat available (spring run) and altering the natural flow regimes (spring run).

Implications for management

Attempts to increase production of Chinook salmon populations in the Central Valley focus entirely on rivers downstream of large dams (United States Fish and Wildlife Service 2001) and there are currently no plans to address passage upstream of these projects (CDWR 2005), although this strategy has been proposed for some rivers (USFWS 1995). Most river restoration projects in the Central Valley are small relative to the scale at which river habitats have been altered, and increases in salmon populations resulting from these efforts may be difficult to detect (Kondolf *et al.* 2008). Large-scale projects such as dam removal may be more effective to recover Chinook salmon populations, but effectiveness is often not the primary criteria used to select what restoration projects will be implemented (Kondolf *et al.* 2008).

Although there is controversy regarding the effectiveness of fish passage above dams and even dam removal as a viable strategy to prevent the extirpation of Chinook salmon (Kareiva *et al.* 2000; Welch *et al.* 2008), dams have strong direct and indirect effects on the growth rate of Chinook salmon populations downstream and increase the probability of future extirpations (McClure *et al.* 2003; Hoekstra *et al.* 2007).These analyses suggest that management of flow regimes downstream of barrier dams could be an important component of conservation efforts to prevent the loss of spring run or to increase the success of recolonisation. Regardless, the evidence that barriers have been one of, if not the, primary driver of Chinook salmon extirpations in the Central Valley seems indisputable.

Chinook populations are at risk of extirpation throughout their range, and populations in interior basins such as the Central Valley are at greater risk than most coastal populations (Gustafson *et al.* 2007). Additionally, the Central Valley represents the southern-most spawning populations of Chinook salmon, and several populations are at high risk of extinction with high biological consequences to the species if they are lost (Allendorf *et al.* 1997). Despite the critical status of Central Valley Chinook, this study is among the first quantitative assessments of the hypothesised drivers of extirpation at a regional scale. A lack of quantitative evaluation is a common problem in salmon management where expert opinion and inferred or extrapolated data are substituted for quantitative measurement and analysis (Ruckelshaus *et al.* 2002). The number of potential hypotheses to explain extirpation of Chinook salmon is large, but data are lacking for most. One advantage of information theoretic methods is that as more data become available, other hypotheses can be quantitatively evaluated against those presented here (Burnham & Anderson 2002). Although some results may appear intuitive, they quantify the importance of addressing large barrier dams that have isolated a large proportion of salmon habitat in the Central Valley; an issue that has yet to be addressed in recovery strategies.

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